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# Trends in the Benthic Macroinvertebrate Community of Saginaw Bay, Lake Huron, 1987 to 1996: Responses to Phosphorus Abatement and the Zebra Mussel, *Dreissena polymorpha*

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***ABSTRACT.*** *Trends in benthic macroinvertebrate populations were examined in inner and outer Saginaw Bay, Lake Huron, from 1987 to 1996. These years represent the time period after phosphorus abatement, but immediately before (1987 to 1990) and after (1991 to 1996) colonization of the bay by the zebra mussel,* Dreissena polymorpha. *In 1987 to 1990, densities of the major macroinvertebrate groups in the inner and outer bay were not significantly different from, or were greater than, densities reported just prior to abatement efforts in the early 1970s. Oligochaete densities in the deepwater/silt region of the inner bay were trending downward between 1988 and 1991, but pollution-tolerant forms dominated the community, indicating the system was eutrophic just prior to* Dreissena *colonization.* Dreissena *impacts on the macroinvertebrate community varied depending on the particular habitat. At shallow-water/sand sites in the inner bay,* Gammarus *increased, and sphaeriids declined after* Dreissena *colonization, but no changes were observed in oligochaetes and chironomids, and overall species diversity showed little change. At deepwater/silt sites in the inner bay, densities of oligochaetes and chironomids declined just after the peak in* Dreissena, *but then returned to levels generally similar to those found prior to* Dreissena. *The oligochaete trophic index at deepwater/silt sites indicated a shift from eutrophic to more oligotrophic indicator species after* Dreissena *became established, and species diversity increased. In the outer bay,* Diporeia *and sphaeriids declined after* Dreissena *peaked, but few other changes were observed. Total non-dreissenid macroinvertebrate biomass (AFDW) in the inner bay, and in shallow areas of the outer bay, did not change as a result of* Dreissena *colonization. On the other hand, biomass in the deeper regions of the outer bay decreased because of the loss of* Diporeia. *Changes in the inner and outer bay typify the growing dichotomy between nearshore and offshore communities in the Great Lakes since* Dreissena *became established.*

***INDEX WORDS:*** *Benthos, community changes, ecological impacts, Saginaw Bay.*

## INTRODUCTION

Prior to the introduction of the dreissenid mussels *Dreissena polymorpha* and *Dreissena bugensis* (zebra mussel and quagga mussel), broad-scale trends in benthic macroinvertebrate communities in nearshore areas of the Great Lakes (< 30 m, shallow bays and basins) were mainly attributed to changes in nutrient loads. Increased inputs of phosphorus up until the mid-1970s led to increased densities of benthic taxa that were tolerant of eutrophic-polluted conditions, while densities of less-tolerant taxa declined (see Cook and Johnson 1974 for review). After phosphorus abatement programs in the mid-1970s, abundances generally declined, and communities in many nearshore areas shifted back to taxa more indicative of an improved trophic state (Johnson and McNeil 1986, Kreiger and Ross 1993, Schloesser *et al.* 1995, Kilgour *et al.* 2000).

The introduction and proliferation of dreissenid mussels has complicated the interpretation of benthic community trends relative to changes in nutrient loads and system productivity. Because of large standing stocks and high filtering rates, dreissenids have altered normal pathways of energy flow from pelagic to benthic regions (Nalepa and Fahnenstiel 1995), or have physically altered benthic habitats (Bially and MacIsaac 2000). Impacts on the

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macroinvertebrate community have varied depending upon particular habitat, spatial proximity to mussel colonies, and taxa initially present. In nearshore, hard-substrate regions, abundances of many taxa have increased in response to the increase in habitat complexity created by mussel colonies, and/or to the increase in food availability from mussel biodeposits (Wisenden and Bailey 1995, Botts *et al.* 1996, Howell *et al.* 1996, Ricciardi *et al.* 1997). In deeper, offshore regions, the response has generally led to a decline in abundances, likely because mussels in nearshore areas sequester food resources that normally would settle in depositional zones (Nalepa *et al.* 1998, Lozano *et al.* 2001). Other studies have shown no change in benthic standing stocks after *Dreissena* colonization (Johannsson *et al.* 2000), or the positive response for many taxa was short term, even in hard-substrate, nearshore regions (Haynes *et al.* 1999).

In this paper, we document trends in benthic macroinvertebrate populations in Saginaw Bay, Lake Huron between 1987 and 1996, and these trends are examined relative to both phosphorus abatement and the establishment of *Dreissena*. When the sampling surveys were initiated in 1987 and 1988, the objective was to determine if the benthic community in the bay had responded to improvements in water quality that resulted from reductions in phosphorus loads (Bierman *et al.* 1984). Sampling was designed to assess changes since the early 1970s, which was the time period just before abatement efforts. When *Dreissena* became established in Lake St. Clair and rapidly spread through Lake Erie in 1988, it was reasoned that this species would soon become very abundant in Saginaw Bay, and further benthic sampling was initiated in 1990 and continued through 1996 with the objective of assessing changes induced by *Dreissena*. *Dreissena* did become established in the bay in 1991 (Nalepa *et al.* 1995), and thus the 1987 to 1996 sampling period represents the years immediately before and after dreissenid colonization.

## DESCRIPTION OF STUDY SITE

Saginaw Bay is a shallow, well-mixed extension of the western shoreline of Lake Huron (Fig. 1). The bay is 21 to 42 km wide, about 82 km long, and has a drainage basin of about 21,000 $km^2$. Total area of the bay is $2.77 \times 10^9$ $m^2$, and total water volume is $24.54 \times 10^9$ $m^3$. The bay can be functionally divided into an inner and outer region by a line extending along its narrowest width (21 km) from Sand Point to Point Lookout (Fig. 1). A broad shoal and several islands (Charity Islands) near this line provide a natural demarcation between the two regions. Differences in physical and chemical features of the inner and outer bay regions are distinct (Beeton *et al.* 1967, Smith *et al.* 1977). The inner bay has a mean depth of 5.1 m (maximum 14 m), is nutrient-rich, and is heavily influenced by organic inputs from the Saginaw River; the river accounts for over 70% of the total tributary flow into the bay. The outer bay has a mean depth of 13.7 m and is more influenced by the colder, nutrient-poor waters of Lake Huron. The inner bay is well-mixed, but thermal stratification is occasionally observed in deeper water (> 10 m) (Nalepa *et al.* 1996).

Circulation within the inner and outer bay is generally weak; currents average about 7 cm/s in the inner bay and about 11 cm/s in the outer bay (Danek and Saylor 1977). Exchange and flushing of water in the inner and outer bay occurs mainly when winds blow along the long axis of the bay (southwest/northeast). Most water exchange occurs on the northern side of the bay within the deep channel that occurs between Point Lookout and Charity Island. Although some water may exit the inner bay along the southern shoreline, it is of minor significance because of the shallowness of the region (Danek and Saylor 1977).

Bottom substrates within the bay range from mostly cobble/rock to silt. The inner bay has a shallow sand bar that extends along the southeastern side of the bay from the Saginaw River to Charity Island. Another sand bar extends along the northwestern shoreline to Point Au Gres. Both sand bars have irregular areas of cobble with patches of gravel, pebbles, and varying amounts of overlying silt. The bars extend into the shorelines as extensive flats grade to marshes. Water depth between the two sand bars gradually increases to a maximum of 14 m (Fig. 1). The proportion of fine-grained material gradually increases along this depth gradient as a function of sediment deposition (Robbins 1981). At depths greater than 6 m, the substrate consists of fine-grained material (silt and clay) and sediment deposition ranges from 0.04 to 0.70 $g/cm^2$ /yr (Robbins 1981).

In the outer bay, the east shore is rocky, as is the area around Charity Island (Fig 1). The western shore has extensive sandy areas, with rock and clay found near Point Lookout. With increased depth, the substrate is mostly sand with varying amounts of overlying silt.

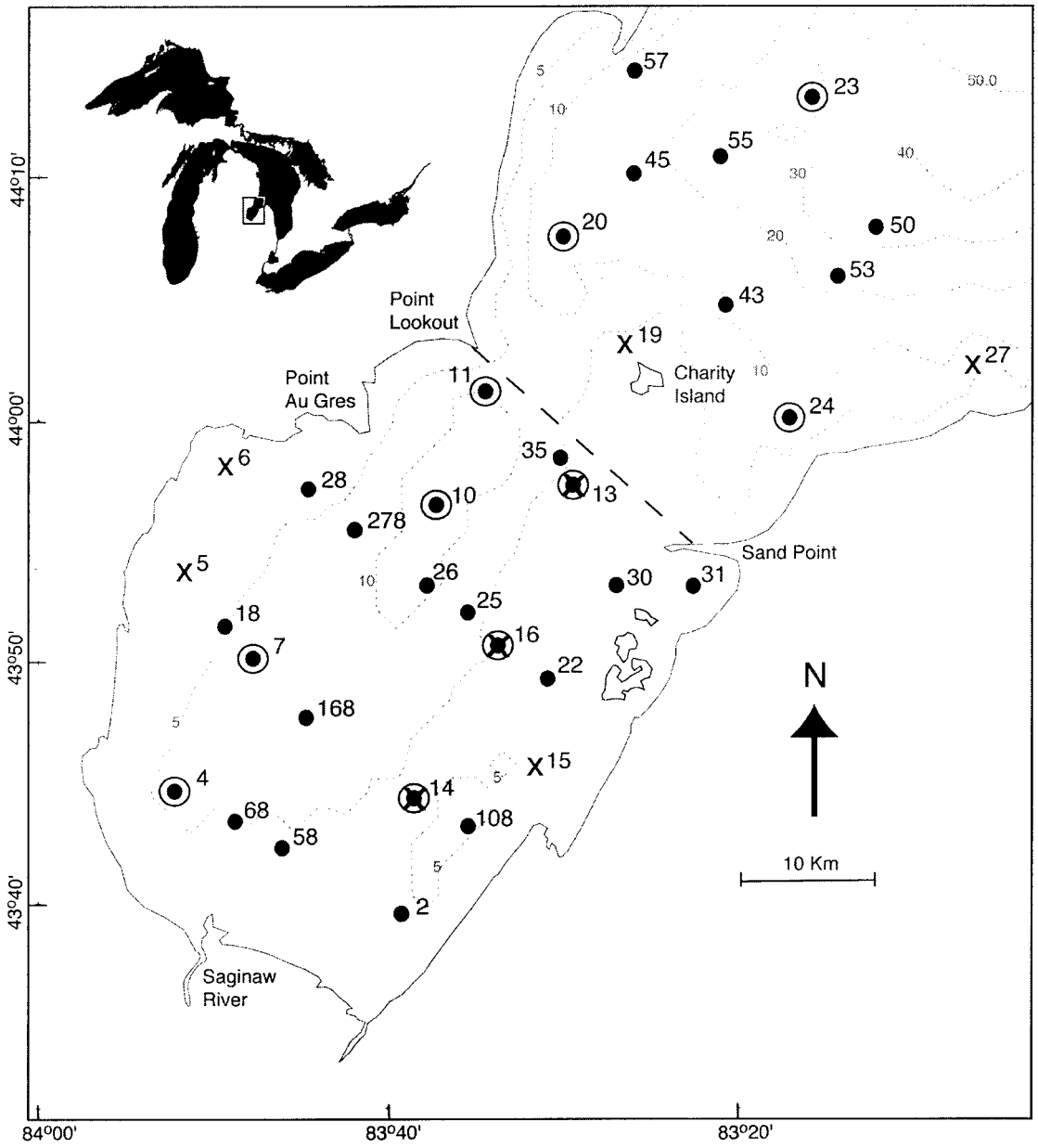


***FIG. 1. Location of sampling sites in Saginaw Bay, 1987 to 1996. Dashed line separates the inner bay from the outer bay. Depth contours are given in meters. • = sampled in 1987 and 1988 only; ⊙ sampled in 1987–1996; X = sampled in 1991-96 for* Dreissena *using SCUBA divers.***

## MATERIALS AND METHODS

### Dates, Locations, and Procedures

Samples for benthic macroinvertebrates were collected at 30 sites in 1987 and 1988, and at 10 sites in 1990 to 1996 (Fig. 1). Samples were collected in spring (May), summer (July), and fall (Sept. to Nov.) of each year except in 1996 when samples were collected only in summer and fall. Because of poor weather or mechanical failures, not all sites were sampled on some dates. Site locations and sampling dates are given in Nalepa *et al.* (2002). Sampling sites were selected by first plotting site locations of previous benthic surveys (Surber 1954, 1955; Schneider *et al.* 1969; Batchelder 1973; Great

Lakes Research Division, University of Michigan, unpublished data), and then choosing the sites to resample based on type of sampler used, detail of data provided, and spatial coverage of the bay.

Triplicate samples were collected at each site with a Ponar grab (area = 0.046 $m^2$). After collection, each sample was washed into a large tub, and then into an elutriation device fitted with a sleeve made of 0.5-mm mesh Nitex (Nalepa *et al.* 1985). Retained material was washed into a collection jar and preserved in 5% buffered formalin containing rose bengal stain. The substrate was visually described prior to rinsing the sample through the Nitex screen (Nalepa *et al.* 1985).

To obtain quantitative estimates of *Dreissena*, samples were collected at eight sites using SCUBA divers every fall from 1991 to 1996 (Fig. 1). Five sites were located in areas with sand/cobble and could not be effectively sampled with the Ponar (Stations 5, 6, 15, 19, 27), while three sites had sand substrates and were sampled by both SCUBA and Ponar (Stations 13, 14, 16). At each site, divers randomly placed a 0.25 or 0.5 $m^2$ frame on the bottom and hand-collected all hard material within the frame area. After all material was removed, the area within the frame was re-sampled using a diver-operated suction device fitted with a Nitex net with 0.5-mm openings (Winnell and Jude 1987). This procedure ensured that all loose mussels were included in the sample. Triplicate samples were collected at each site, with divers moving 2 to 3 m between replicates.

In the laboratory, material collected in the grab and retained by the 0.5-mm sleeve was placed into a white enamel pan and organisms were removed, enumerated, and sorted into major groups (Amphipoda, Oligochaeta, Sphaeriidae, Chironomidae, *Dreissena*, and others) under a 1.5× lighted magnifier lamp. Turbellarians and nematodes were observed in the samples but, since methods were not quantitative for these groups, their numbers were not recorded. When the number of organisms in a sample was extremely large, the sample was proportionately split and only a portion was processed. All organisms were identified to the lowest practical taxonomic level. For oligochaetes, between 75 and 100 individuals in a replicate (proportionately split with a Folsom plankton splitter when numbers were high) were cleared in lactophenol before identification. Oligochaetes were mounted on microscope slides (in glycerine) and their images were projected onto a sheet of paper using a camera lucida and then traced. Individuals were identified, and taxonomic designations placed alongside the respective traced image. Only individuals with a prostomium were identified and tabulated; fragments (without prostomium) were identified as such but were not counted. For chironomids, a maximum of 50 individuals were identified per replicate. Head capsules were teased off the body, cleared in lactophenol, and mounted on microscope slides with mentum side up. The corresponding body was mounted alongside the head capsule and the image traced as for oligochaetes.

Biomass (ash-free dry weight [AFDW]) for Amphipoda, Isopoda, Ephemeroptera, Oligochaeta, Chironomidae, and *Dreissena* were derived from length-weight relationships determined either directly on fresh animals, or taken from the literature. If a length-weight relationship for a given taxon was not available from the literature, it was assigned the relationship of a closely-related form (Nalepa *et al.* 2002). When length-weight relationships were available for only dry weight, ash-free dry weight was assumed to be 90% of dry weight (Johnson and Brinkhurst 1971). Weights were determined by placing fresh animals into pre-weighted, aluminum planchets, dried at 60°C for 48 h, and weighed to the nearest 0.1 mg. AFDW was obtained by re-weighing the specimens after ashing at 550°C for 1 h. Lengths were measured directly or determined from traced images using a digitizer (Quigley and Lang 1989).

For oligochaetes, all body fragments present on the slides were measured and included in the biomass total. Length-weight conversions are based on the finding that preservation does not alter length (Erman and Erman 1975). For *Dreissena*, lengths were measured on up to 500 animals in each sample using a computer scanner and fitted software. If more individuals were present in the sample, the sample was proportionately split. To determine length-weight of *Dreissena*, at least 25 individuals of various sizes were collected in fall at Station 5 in 1991 to 1996, and at Station 19 in 1994 to 1996. Annual biomass is best derived from a length-weight determined in the fall when spawning has been completed (Nalepa *et al.* 1993). Shell lengths were measured, and AFDW of the soft tissue was determined as above. Corresponding length-weight relationships were determined and then used to calculate soft-tissue biomass of mussels at the various sites. In 1991 to 1993, length-weight relationships derived from mussels collected at Station 5 were used to calculate biomass at all sites, but in 1994 to 1996 separate relationships derived from mussels at

***TABLE 1. Mean density (no./m$^2$ ± SE) of major benthic macroinvertebrate groups in 1987/88. Stations in the inner bay were grouped by substrate (I, II, III), and stations in the outer bay were grouped by depth (IV, V, VI). Differences between the substrate/depth groups for the inner and outer bay were tested for each macroinvertebrate group using ANOVA (ln +1 transformed). ns = not significantly different.***

| Group | Station | Depth (m) | Substrate | Oligochaeta | Chironomidae | Amphipoda | Sphaeriidae | Total |
|---|---|---|---|---|---|---|---|---|
| Inner Bay | | | | | | | | |
| I | 13, 14 16, 18, 28 | 3.0–4.8 | sand/gravel | 1,111 ± 281 | 202 ± 94 | 60 ± 21 | 58 ± 19 | 1,441 ± 374 |
| II | 2, 11, 22, 25, 30, 35, 58, 68, 108 | 4.2–9.0 | silty sand | 5,870 ± 808 | 2,163 ± 801 | 15 ± 7 | 250 ± 49 | 8,327 ± 1,281 |
| III | 4, 7, 10, 26, 168, 278 | 6.7–11.8 | silt | 20,954 ± 1,909 P < 0.01 | 1,412 ± 159 P < 0.01 | <1 ± <1 P < 0.01 | 86 ± 19 P < 0.01 | 21,951 ± 2,019 P < 0.01 |
| Outer Bay | | | | | | | | |
| IV | 24, 43, 57 | 10–13 | silty sand | 4,952 ± 659 | 4,559 ± 439 | 117 ± 5 | 385 ± 298 | 10,025 ± 84 |
| V | 20, 45, 53 ,55 | 16–22 | silty sand | 3,043 ± 300 | 1,010 ± 282 | 93 ± 39 | 189 ± 72 | 4,337 ± 306 |
| VI | 23, 50 | 28–30 | silty sand | 2,304 ± 1,094 ns | 191 ± 44 P < 0.01 | 1,209 ± 254 P < 0.05 | 222 ± 45 ns | 3,982 ± 1,159 P < 0.01 |

Station 5 and Station 19 were used to calculate biomass at sites in the inner bay and outer bay, respectively.

AFDW of other benthic taxa (Sphaeriidae, Gastropoda, Trichoptera, Isopoda, Hirudinea, and Diptera other than Chironomidae) was determined directly from preserved specimens within a given sample. While preservation does not cause weight loss in Sphaeriidae (Johnson and Brinkhurst 1971), weight loss likely occurred in the other taxa. However, these taxa generally constituted only a small portion of total biomass at a given site. Further details of biomass determinations, including length-weight regressions, are given in Nalepa *et al.* (2002).

### Site Groupings and Analysis

To examine benthic responses to abatement efforts, data collected in 1987 to 1990 (post abatement and pre-*Dreissena)* were compared to data from two surveys conducted in the early 1970s (pre-abatement). One survey occurred mainly in the inner bay (in 1971; Batchelder 1973), and the other occurred in the outer bay (in 1972; Great Lakes Research Division [GLRD], University of Michigan, unpublished data). Sampling methods in both surveys were similar to that of this study; that is, the collection device was the Ponar grab, and samples were washed through a 500–600-µm screen. We matched our sites with sites sampled in 1971 based on substrate, water depth, and general location, while our site locations matched 1972 site locations exactly since the 1972 coordinates were incorporated into the original sampling design. When testing for differences between the two time periods within a given substrate, each site pairing was considered a separate replicate.

Substrates at the twenty-one sites sampled with the Ponar grab in the inner bay varied from coarse sand/gravel to silt, and water depths ranged from 3.0 to 11.8 m (Nalepa *et al.* 2002). As found by others (Wood 1964, Robbins 1981), the amount of fine-grained material increased with water depth. For purposes of data analysis, sites in the inner bay were grouped into three categories based on water depth and substrate type: 1) sand/gravel, 3.0 to 4.8 m; 2) silty sand, 4.2 to 9.0 m; and 3) silt, 6.7 to 11.8 m (Table 1). The only site that did not fit into one of these categories was Station 31. Water depth at this site was only 3.2 m, but the substrate differed from all other sites, consisting of coarse plant debris/silt. This site was located in the center of a shallow, confined embayment (Wildfowl Bay) and

was not representative of the bay in general. With this exception, sites in these three categories were located in regions considered to be non-depositional, transitional, and depositional, respectively (Robbins 1981). In the outer bay, substrates consisted of silty sand at all sites, and depths ranged from 10 to 30 m (Nalepa *et al.* 2002). Since substrates were generally the same, the nine outer bay sites were grouped into three categories based on water depth: 10 to 13 m, 16 to 22 m, and 28 to 30 m (Table 1). These depth categories are consistent with prior characterization of depth-macroinvertebrate associations in other regions of the Great Lakes for similar depths and substrate types (Cook and Johnson 1974, Mozley and Howmiller 1977).

As noted, only ten sites were sampled in 1990 to 1996, but these sites were considered to be representative of the various habitat types. In the inner bay, three sites were in the shallow water/sand region (Stations 13, 14, 16), one site was in the mid-depth/silty sand region (Station 11), and three sites were in the deep water/silt region (Stations 4, 7, and 10) (Fig. 1). In the outer bay, sampling was continued at three sites, each within the three depth intervals: 13 m (Station 24), 16 m (Station 20), and 28 m (Station 23).

When testing for benthic macroinvertebrate responses to *Dreissena* colonization, the 1987 to 1990 period was considered as the pre-*Dreissena* period, and 1993 to 1996 was considered as the post-*Dreissena* period. While data collected in 1991 and 1992 were included when interpreting trends, these 2 years were considered transitional and not included in the statistical analysis. That is, *Dreissena* was present for only part of the year in 1991, and abundances were at unsustainably high levels in 1992 (Nalepa *et al.* 1995). Only data collected at the ten sites sampled every year were used to assess *Dreissena* impacts. The mean of each year was considered an individual replicate, and differences between periods were tested using a t-test. Abundance data were ln +1 transformed prior to any statistical analysis (t-tests and ANOVAs) and met the requirements of normality and equality of variances.

Species composition of the oligochaete community is a good indicator of trophic status, and community changes were examined using an oligochaete trophic index (Howmiller and Scott 1977, Milbrink 1983, Lauritsen *et al.* 1985). The index is determined by placing each species (excluding Naididae and Enchytraeidae) into one of four categories based on its tolerance to organic enrichment. Values of each category range from 0 (intolerant of enrichment; found mostly in oligotrophic conditions) to 3 (tolerant of enrichment; found in highly eutrophic conditions). The assigned category of each species follows that of Milbrink (1983) and Lauritsen *et al.* (1985). To obtain the index, the number of individuals in each category is multiplied by the category value (species in category 0 are assigned a value of 0.5). The products are then summed and divided by the total number of individuals.

The Simpson Diversity Index (Simpson 1949) and the Bray Curtis Index (Bray and Curtis 1957) were used to determine changes in structure of the entire macroinvertebrate community. The former index considers both taxonomic richness and evenness, while the latter considers presence/absence and absolute abundance of each taxa. Of the many similarity indices, the Bray-Curtis Index has been shown to be the most effective quantitative index when assessing changes in community structure (Hruby 1987, Pontasch and Brusven 1988, Pontasch *et al.* 1989). Since the index is sensitive to occasional large numbers, data were square-root transformed prior to index calculation (Pontasch and Brusven 1988). Both indices were determined on the non-dreissenid community.

## RESULTS

### General Distribution Patterns in 1987 and 1988

Since 30 sites were sampled in 1987 and 1988 and these sites provided broad spatial coverage of the bay, data collected in these 2 years were used to characterize general distribution patterns. Total mean densities in the inner bay generally increased with water depth and the amount of fine-grained material (Table 1, Fig. 2). Mean densities at sites with sand, silty sand, and silt substrates were 1,441, 8,327, and 21,951/$m^2$, respectively. Differences were significant for all major macroinvertebrate groups (ANOVA, $P < 0.01$) (Table 1). Oligochaetes, chironomids, and sphaeriids were more abundant at sites with sandy silt or silt substrate, while the amphipod *Gammarus* sp. was most abundant at sites with sand. In terms of composition, oligochaetes were the dominant group in all three substrates, accounting for 77 to 95% of all organisms collected. Dominant species in silt were *Limnodrilus hoffmeisteri* and *Limnodrilus cervix*, while the naidids *Piguetiella michiganensis*, *Uncinais uncinata*, and *Arcteonais lomondi* were the most common species in sand. Most abundant chironomid species


***FIG. 2. Mean total density (no./m$^2$ × 10$^3$) of benthic macroinvertebrates in Saginaw Bay, 1987 and 1988.***

were *Cladotanytarsus* spp. and *Tanytarsus* sp. in sand, *Chironomus anthracinus*, *Tanytarsus* sp., and *Procladius* sp. in silty sand, and *Chironomus semireductus-gr.* and *C. anthracinus* in silt.

In the outer bay, total density declined, and the community shifted to species more typical of a cold-water environment as depth increased. The greatest depth-related change occurred in chironomids (Table 1). Chironomid densities declined from 4,559/m$^2$ at the 10 to 13 m interval to 191/m$^2$ at the 28 to 30 m interval ($P < 0.01$). *Tanytarsus* sp., *Paratendipes* sp., and *C. anthracinus* were the dominant taxa at the shallower sites, while *Heterotrissocladius* spp. was dominant at the deeper sites. The amphipod *Diporeia* spp. was most abundant at the deepest interval ($P < 0.01$). Both *Heterotrissocladius* and *Diporeia* are typically found in the colder, deeper regions of the Great Lakes; both species were rarely found in the inner bay. Total densities of both oligochaetes and sphaeriids were not related to depth ($P > 0.05$). At least for the former group, this was partly attributable to high densities at one of the sites in the deepest interval, Station 50. Mean oligochaete density at this site was 4,100/m$^2$, compared to just 430/m$^2$ at the other site within this interval, Station 23. This difference could be attributed to high numbers of tubificids at Station 50 (82% of all oligochaetes), of which *Potamothrix vejdovskyi* and *L. hoffmeisteri* were the dominant species. Based on typical exchange rates and flow patterns from the inner bay to the outer bay (Danek and Saylor 1977), the community at Station 50 was more likely influenced by nutrient-rich waters from the inner bay than the community at Station 23. Both chlorophyll and total suspended matter was consistently higher at the former station compared to the latter (Nalepa *et al.* 1996). Both *P. vejdovskyi* and *L. hoffmeisteri* do well in enriched environments (Milbrink 1983). In contrast, the dominant oligochaete species at Stations 23 was *Stylodrilus heringinaus*, an oligotrophic, cold-water form.

### Comparisons Pre- and Post-Phosphorus Abatement

A total of twelve sites sampled in the inner bay in 1987 to 1990 (post abatement) were matched with sites sampled in 1971 by Batchelder (1973) (pre-abatement). Comparisons of the major benthic groups indicated that mean densities in 1987 to 1990 were generally similar to, or greater than, densities in 1971 (Table 2). In terms of species composition, only the chironomid community could be compared since oligochaetes were not identified to species in 1971. Further, only broad, generic comparison of the chironomid community was possible because of uncertainties with nomenclature and level of taxonomic detail given for the 1971 data. Dominant chironomid taxa in 1971 were *Tanytarsus* sp. (50%) and *Polypedilum* spp. (31%) in sand, *Chironomus* spp. (41%) and *Procladius* spp. (34%) in silty sand, and *Chironomus* spp. (93%) in silt (Batchelder 1973). For the same sites, dominant species in 1987 to 1990 were *Cladotanytarus* spp. (25%) and *Tanytarsus* sp. (23%) in sand, *Chironomus* spp. (47%), *Tanytarsus* sp. (30%) and *Procladius* sp. (12%) in silty sand, and *Chironomus* spp. (95%) in silt.

In the outer bay, five of the sites sampled in 1987 to 1990 corresponded to sites that were sampled in 1972 (Table 3). A comparison of densities in the two sampling periods indicated that all differences in the major groups were non signifi-

***TABLE 2. Mean densities (no./m²) of major benthic macroinvertebrate groups in 1971 and 1987 to 1990 in inner Saginaw Bay by substrate type. The 1971 data were taken from Batchelder (1973). Stations sampled in the two time periods were paired based on general station location, water depth, and substrate type. Station designations of Batchelder (1973) are given in parenthesis. Density differences between periods were tested for each substrate type using paired t-test after ln +1 transformation with each site pairing considered a replicate. Station 31 was not included in the analysis (see text). * = significantly different at P < 0.05.***

| Substrate/ | Oligochaeta | | Chironomidae | | Amphipoda | | Sphaeriidae | |
|---|---|---|---|---|---|---|---|---|
| Station | 1971 | 1987–90 | 1971 | 1987–90 | 1971 | 1987–90 | 1971 | 1987–90 |
| Sand | | | | | | | | |
| 13 (29) | 1,587 | 908 | 570 | 136 | 215 | 104 | 43 | 27 |
| 14 (24) | 1,033 | 516 | 323 | 140 | 215 | 38 | 0 | 33 |
| 18 (21) | 1,689 | 2,168 | 1,700 | 524 | 0 | 5 | 0 | 136 |
| Mean | 1,436 | 1,197 | 764 | 267* | 143 | 49 | 14 | 65 |
| ± SE | ± 204 | ± 498 | ± 493 | ± 129 | ± 72 | ± 29 | ± 14 | ± 35 |
| Silty Sand | | | | | | | | |
| 2 (20) | 10,706 | 6,696 | 1,452 | 2,626 | 0 | 8 | 0 | 74 |
| 30 (30) | 8,619 | 10,230 | 624 | 2,157 | 0 | 8 | 0 | 343 |
| 11 (32) | 2,303 | 6,799 | 554 | 6,941 | 0 | 6 | 0 | 535 |
| 108 (25) | 4,100 | 5,269 | 484 | 1,510 | 0 | 2 | 0 | 60 |
| Mean | 6,432 | 7,249 | 779 | 3,309* | 0 | 6* | 0 | 253* |
| ± SE | ± 1,948 | ± 1,053 | ± 226 | ± 1,232 | ± 0 | ± < 1 | ± 0 | ± 114 |
| Silt | | | | | | | | |
| 4 (18) | 14,956 | 22,380 | 1,668 | 1,790 | 0 | 0 | 0 | 86 |
| 7 (22) | 12,008 | 15,299 | 2,216 | 1,338 | 0 | 1 | 0 | 141 |
| 10 (28) | 16,151 | 18,582 | 4,541 | 1,307 | 22 | 1 | 0 | 53 |
| 168 (23) | 11,534 | 13,313 | 1,571 | 749 | 0 | 2 | 43 | 7 |
| Mean | 13,662 | 17,394* | 2,499 | 1,296 | 6 | 1 | 11 | 72 |
| ± SE | ± 1,123 | ± 1,986 | ± 602 | ± 213 | ± 5 | ± < 1 | ± 11 | ± 28 |
| Silt: Wildfowl Bay | | | | | | | | |
| 31 (31) | 4,882 | 19,337 | 1,799 | 1,746 | 0 | 44 | 0 | 0 |

cant (paired t-test, P > 0.05). Further, the oligochaete trophic index indicated the community was dominated by oligotrophic species in both time periods. Index values (mean ± SE) were 0.96 ± 0.05 in 1972 and 1.02 ± 0.02 in 1987–90. Dominant species were *Spirosperma ferox*, *Aulodrilus pluriseta*, and *S. heringianus*; these three species accounted for 92% of all oligochaetes in 1972 and 65% in 1987 to 1990. Other abundant species in the latter period were *P. vejdovskyi* (10%), *L. hofmeisteri* (6%), and *Aulodrilus americanus* (3%). For chironomids, *Tanytarsus* sp. was the dominant species in both periods (45% of all chironomids). Differences in Simpson's Diversity Index between the two periods were non-significant (paired t-test, P > 0.05).

**Trends and Comparisons, Pre- and Post-Dreissena**

*Dreissena* was initially found in samples from spring 1991, and the first large recruitment occurred that summer (Nalepa *et al.* 1995). Mean densities on cobble/sand in the inner bay, as sampled by divers, reached a maximum of 33,838/m² in 1992, declined in 1993, and then varied between 2,100 and 5,500/m² from 1993 to 1996 (Table 4). Few mussels were found at sites with silty sand or silt substrate during the entire sampling period. Densities tended to be higher in the outer bay than in the inner bay, but this was likely a result of greater amounts of hard substrate (cobble, bedrock) found at the outer bay sites. Mean biomass for 1993 to 1996 varied between 4.1 and 13.4 g/m² in the inner bay, and between 13.8 and 97.8 g/m² in the outer bay (Table 4). Greater biomass occurred at sites in

***TABLE 3. Mean densities (no./m²) of major benthic macroinvertebrate groups in 1972 and 1987 to 1990 in outer Saginaw Bay. The 1972 data were provided by the Great Lakes Research Division, University of Michigan (GLRD unpublished). Station coordinates were similar for the two sampling periods. Station designations in 1972 are given in parenthesis. Mean differences between the two time periods were tested using paired t-test after ln +1 transformation (n = 5). All differences were non-significant (P > 0.05).***

| | | Oligochaeta | | Chironomidae | | Amphipoda | | Sphaeriidae | |
|---|---|---|---|---|---|---|---|---|---|
| Station | Depth (m) | 1972 | 1987–90 | 1972 | 1987–90 | 1972 | 1987–90 | 1972 | 1987–90 |
| 57 (57) | 10 | 5,647 | 5,184 | 981 | 3,366 | 287 | 173 | 688 | 385 |
| 20 (62) | 16 | 12,849 | 1,894 | 738 | 1,383 | 186 | 3 | 1,226 | 372 |
| 45 (63) | 18 | 3,841 | 2,949 | 1,820 | 1,609 | 1,712 | 571 | 1,125 | 92 |
| 53 (53) | 22 | 4,644 | 4,324 | 380 | 380 | 752 | 338 | 72 | 123 |
| 55 (55) | 22 | 3,698 | 3,240 | 344 | 563 | 4,106 | 1,523 | 1,003 | 156 |
| | Mean | 6,136 | 3,518 | 851 | 1,460 | 1,409 | 522 | 823 | 226 |
| | ± SE | ± 1,713 | ± 568 | ± 269 | ± 531 | ± 726 | ± 267 | ± 208 | ± 63 |

***TABLE 4. Mean densities (no./m² ± SE) and biomass (g AFDW/m2; in parenthesis) of Dreissena polymorpha on various substrate types in inner and outer Saginaw Bay. Sites with cobble/sand and cobble/bedrock were sampled using SCUBA, and other sites were sampled with a Ponar grab. Biomass estimated only for sites sampled with SCUBA. Densities and biomass estimated in the fall of each year. n = number of stations.***

| Location/ Substrate | Year n | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 |
|---|---|---|---|---|---|---|---|
| Inner Bay | | | | | | | |
| Cobble/Sand | 6 | 15,210 ± 8,718 (10.02) | 33,838 ± 13,003 (61.87) | 3,975 ± 1,312 (4.49) | 4,982 ± 1,716 (8.33) | 2,145 ± 1,009 (4.09) | 5,548 ± 2,663 (13.39) |
| Silty Sand | 1 | 0 | 45 | 1,268 | 29 | 114 | 18 |
| Silt | 3 | 14 ± 7 | 9 ± 9 | 37 ± 26 | 43 ± 36 | 2 ± 2 | 7 ± 7 |
| Outer Bay | | | | | | | |
| Cobble/ Bedrock | 2 | 2,944 ± 464 (0.65) | 31,168 ± 26,473 (53.85) | 4,570 ± 1,243 (13.79) | 15,797 ± 5,872 (44.54) | 10,800 ± 6,976 (63.19) | 13,165 ± 6,184 (97.76) |
| Silty Sand | 3 | 0 ± 0 | 2 ± 2 | 5 ± 5 | 0 ± 0 | 0 ± 0 | 0 ± 0 |

the outer bay not only because of higher densities, but also because the mussels were larger and weighed more per unit length (Nalepa *et al.* 2002). While mussel densities in the outer bay were generally consistent between 1994 and 1996, biomass increased as a result of an increase in mean size (Nalepa unpublished data).

The response of the benthic community to *Dreissena* colonization varied depending upon substrate type and water depth. At shallower sites with sand or silty sand substrates in the inner bay, densities of only two taxa changed significantly relative to the establishment of *Dreissena* (Table 5). At these sites, densities of *Gammarus* were significantly higher ($P < 0.05$), and densities of sphaeriids were significantly lower ($P < 0.05$) in the post-*Dreissena* period (1993 to 1996) compared to the pre-*Dreissena* period (1987 to 1990). Densities of both oligochaetes and chironomids were not significantly different between the two periods ($P > 0.05$). Mean annual densities of both groups were highly variable at the site with silty sand (Station 11) in the pre-*Dreissena* period, which may explain the lack of statistical significance between the pre-and post-*Dreissena* periods (Table 5). But even so, densities of both groups were relatively stable between 1991 and 1996 and unaffected by the peak and decline in *Dreissena* over that time period. Since oligochaetes and chironomids, as well as *Gammarus*, are consistently more abundant in mussel clusters than in surrounding substrates (Karatayev *et al*. 1997), the relationship between densities of these groups and

***TABLE 5. Mean density (no./m² ± SE) of major macroinvertebrate groups (excluding* Dreissena*) collected from different substrates in the inner bay and from different water depths in the outer bay in 1987 to 1996. Stations given in parenthesis.***

| | Year | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1987 | 1988 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 |
| Inner Bay | | | | | | | | | |
| Sand (13,14,16)[a] | | | | | | | | | |
| Oligochaeta | 835 ± 180 | 683 ± 281 | 442 ± 40 | 823 ± 84 | 316 ± 43 | 524 ± 52 | 494 ± 159 | 722 ± 73 | 932 ± 129 |
| Chironomidae | 140 ± 55 | 48 ± 24 | 129 ± 25 | 390 ± 158 | 74 ± 29 | 299 ± 122 | 71 ± 31 | 45 ± 8 | 328 ± 194 |
| Amphipoda | 72 ± 25 | 84 ± 46 | 40 ± 15 | 74 ± 30 | 37 ± 10 | 494 ± 145 | 240 ± 65 | 259 ± 150 | 390 ± 235 |
| Sphaeriidae | 24 ± 18 | 40 ± 17 | 17 ± 11 | 40 ± 25 | 13 ± 7 | 16 ± 14 | 6 ± 3 | 3 ± 1 | 8 ± 8 |
| Other | 0 | 26 ± 14 | 32 ± 20 | 29 ± 6 | 3 ± 2 | 37 ± 16 | 8 ± 4 | 3 ± 2 | 17 ± 13 |
| Total | 1,071 ± 174 | 882 ± 356 | 659 ± 48 | 1,361 ± 227 | 443 ± 80 | 1,371 ± 207 | 819 ± 209 | 1,030 ± 166 | 1,676 ± 381 |
| Silty Sand (11)[b] | | | | | | | | | |
| Oligochaeta | 10,758 ± 5,567 | 7,104 ± 164 | 2,535 ± 1,218 | 1,457 ± 345 | 3,023 ± 1,530 | 1,616 ± 360 | 2,232 ± 222 | 4,627 ± 3,099 | 2,945 ± 75 |
| Chironomidae | 1,652 ± 779 | 15,362 ± 7,836 | 3,811 ± 1261 | 1,480 ± 666 | 4,489 ± 3,164 | 902 ± 367 | 1,269 ± 300 | 3,232 ± 2,134 | 1,935 ± 764 |
| Amphipoda | 5 ± 2 | 0 | 14 ± 0 | 12 ± 5 | 17 ± 13 | 81 ± 54 | 57 ± 25 | 43 ± 39 | 54 ± 11 |
| Sphaeriidae | 490 ± 71 | 664 ± 79 | 450 ± 57 | 455 ± 258 | 395 ± 120 | 835 ± 281 | 74 ± 30 | 50 ± 31 | 225 ± 39 |
| Other | 0 | 0 | 5 ± 2 | 10 ± 2 | 0 | 36 ± 18 | 12 ± 2 | 0 | 14 ± 7 |
| Total | 12,904 ± 5,954 | 23,130 ± 7,750 | 6,813 ± 744 | 3,412 ± 1,190 | 7,923 ± 4,761 | 3,470 ± 853 | 3,644 ± 215 | 7,951 ± 5,253 | 5,173 ± 746 |
| Silt (4,7,10) [a] | | | | | | | | | |
| Oligochaeta | 19,387 ± 4,058 | 21,195 ± 1,672 | 15,678 ± 2,587 | 7,929 ± 511 | 7,056 ± 285 | 1,722 ± 383 | 1,208 ± 348 | 2,355 ± 1,115 | 4,618 ± 1,682 |
| Chironomidae | 1,944 ± 329 | 1,302 ± 10 | 1,289 ± 308 | 1,346 ± 124 | 1,190 ± 200 | 817 ± 209 | 603 ± 66 | 2,206 ± 698 | 2,893 ± 984 |
| Amphipoda | 0 | 1 ± 1 | 1 ± 1 | 5 ± 5 | 4 ± 4 | 9 ± 2 | 16 ± 6 | 14 ± 1 | 6 ± 1 |
| Sphaeriidae | 100 ± 28 | 139 ± 51 | 40 ± 6 | 94 ± 34 | 76 ± 35 | 334 ± 111 | 159 ± 64 | 40 ± 31 | 253 ± 151 |
| Other | 0 | 1 ± 1 | 0 | 1 ± 1 | 0 | 0 | 0 | 0 | 1 ± 1 |
| Total | 21,433 ± 4364 | 22,639 ± 1633 | 17,008 ± 2900 | 9,376 ± 614 | 8,326 ± 456 | 2,881 ± 497 | 1,973 ± 349 | 4,605 ± 1475 | 7,772 ± 2,621 |
| Outer Bay | | | | | | | | | |
| 13 m (24) [b] | | | | | | | | | |
| Oligochaeta | 5,581 ± 1936 | 2,517 ± 1839 | 1,169 ± 185 | 1,792 ± 559 | 1,454 ± 849 | 1,100 ± 778 | 878 ± 294 | 4,370 ± 470 | 1,489 ± 296 |
| Chironomidae | 840 ± 461 | 1,510 ± 1,246 | 519 ± 171 | 593 ± 184 | 797 ± 384 | 685 ± 557 | 386 ± 116 | 3,823 ± 3,066 | 725 ± 632 |
| Amphipoda | 12 ± 6 | 7 ± 7 | 7 ± 7 | 10 ± 6 | 10 ± 6 | 32 ± 19 | 14 ± 8 | 0 | 43 ± 14 |
| Sphaeriidae | 26 ± 13 | 75 ± 39 | 24 ± 13 | 57 ± 26 | 40 ± 25 | 57 ± 36 | 2 ± 2 | 15 ± 9 | 0 |
| Other | 0 | 0 | 2 ± 2 | 0 | 5 ± 5 | 0 | 2 ± 2 | 0 | 0 |
| Total | 6,459 ± 2,346 | 4,109 ± 3,038 | 1,721 ± 234 | 2,451 ± 631 | 2,306 ± 1219 | 1,874 ± 1,353 | 1,283 ± 374 | 8,209 ± 3147 | 2256 ± 321 |
| 16 m (20) [b] | | | | | | | | | |
| Oligochaeta | 2,454 ± 1017 | 2,430 ± 1,069 | 797 ± 275 | 659 ± 145 | 1,473 ± 175 | 1,196 ± 321 | 1,366 ± 723 | 4,127 ± 963 | 2,253 ± 425 |
| Chironomidae | 1,568 ± 1,009 | 1,401 ± 448 | 1,171 ± 345 | 778 ± 529 | 605 ± 322 | 646 ± 227 | 486 ± 159 | 2,306 ± 1,325 | 2,598 ± 1,985 |
| Amphipoda | 7 ± 4 | 0 | 2 ± 2 | 0 | 0 | 13 ± 10 | 12 ± 2 | 12 ± 9 | 7 ± 7 |
| Sphaeriidae | 107 ± 77 | 666 ± 296 | 345 ± 361 | 109 ± 29 | 50 ± 27 | 98 ± 68 | 98 ± 77 | 100 ± 25 | 60 ± 18 |
| Other | 2 ± 2 | 0 | 2 ± 2 | 0 | 0 | 2 ± 2 | 0 | 0 | 0 |
| Total | 4,139 ± 1,900 | 4,498 ± 1,668 | 2,318 ± 845 | 1,547 ± 625 | 2,128 ± 437 | 1,955 ± 368 | 1,961 ± 940 | 6,545 ± 2,303 | 4919 ± 2399 |
| 28 m (23) [b] | | | | | | | | | |
| Oligochaeta | 482 ± 175 | 469 ± 178 | 212 ± 66 | 569 ± 192 | 202 ± 52 | 246 ± 75 | 431 ± 10 | 792 ± 233 | 957 ± 21 |
| Chironomidae | 252 ± 156 | 281 ± 97 | 121 ± 23 | 50 ± 14 | 45 ± 2 | 134 ± 27 | 233 ± 66 | 707 ± 397 | 607 ± 514 |
| Amphipoda | 574 ± 401 | 1,190 ± 536 | 693 ± 84 | 1,154 ± 824 | 240 ± 178 | 591 ± 62 | 371 ± 32 | 50 ± 39 | 82 ± 32 |
| Sphaeriidae | 219 ± 135 | 350 ± 31 | 114 ± 29 | 93 ± 46 | 50 ± 25 | 66 ± 34 | 102 ± 29 | 167 ± 71 | 336 ± 57 |
| Other | 107 ± 50 | 109 ± 13 | 98 ± 77 | 7 ± 7 | 7 ± 7 | 4 ± 4 | 0 | 0 | 0 |
| Total | 1,634 ± 880 | 2,399 ± 338 | 1,238 ± 243 | 1,873 ± 964 | 545 ± 235 | 1,040 ± 338 | 1,138 ± 81 | 1716 ± 542 | 1985 ± 628 |

[a] SE = variability between station means
[b] SE = variability between season means

*Dreissena* was examined by using correlation analysis. Only those replicate samples taken in the post-*Dreissena* period (1993 to 1996) and with *Dreissena* present were used in the analysis. Pearson correlation coefficients between densities of oligochaetes and chironomids and *Dreissena* were not significant ($P > 0.05$; oligochaete coefficient = 0.13, n = 96; chironomid coefficient = –0.05, n = 96). In contrast, a similar analysis for *Gammarus*, was highly significant ($P < 0.01$; coefficient = 0.61; n = 62).

Species composition of both oligochaetes and chironomids were generally unaffected by *Dreissena* at sites with sand and silty sand substrates. The oligochaete trophic index remained generally constant over the entire sampling period at sites with both substrates (Fig. 3a). The index does not include Naididae, however, and this family dominated the oligochaete community at sites with sand. A further examination of naidids indicated some changes in the relative proportion of individual species, although the total number of taxa was similar in the pre-and post-*Dreissena* periods (7 and 10, respectively). The proportion of the following species changed the most between the two periods: *Arcteonais lomondi* and *Chaetogaster* sp. decreased (14.0% to 1.2%; 13.6% to 0.1%) and *Piguetiella michiganensis* increased (40.2% to 70.0%). For chironomids, a total of 19 and 24 taxa were collected in the pre- and post-*Dreissena* periods, respectively, and the dominant species was *Cladotanytarsus mancus* in both periods (42.8% and 69.1%). Temporal trends in Simpson's Diversity Index relative to *Dreissena* colonization were not apparent (Fig. 3b).

At sites in the deepwater/silt region, oligochaete densities were significantly lower ($P < 0.01$) in the post-*Dreissena* period compared to the pre-*Dreissena* period, but differences in the other groups were not apparent ($P > 0.05$). Oligochaetes declined from a peak of 21,195/$m^2$ in 1988 to a low of 1,208/$m^2$ in 1994, and then increased to 4,618/$m^2$ by 1996. Greatest proportional declines occurred between 1990 and 1991 (50%), and between 1992 and 1993 (76%). While the latter decline followed the *Dreissena* peak, it seems unlikely that the former decline could be attributed entirely to *Dreissena*. Mean oligochaete density was 17,749/$m^2$ in fall 1990, but only 7,758/$m^2$ in spring 1991. Thus, oligochaete densities were already much lower in spring 1991 even before the major *Dreissena* colonization occurred in summer 1991.

Tubificid oligochaetes comprised 99% and 90% of all oligochaetes in the pre- and post-*Dreissena* periods, respectively, at sites in the deepwater/silt region, and the oligochaete trophic index indicated a distinct shift from eutrophic to mesotrophic species after *Dreissena* colonization (Fig. 3a). The mean index value declined from 2.14 ± 0.12 to 1.72 ± 0.09 ($P < 0.05$). The proportion of the following species indicative of considerable enrichment decreased: *L. hoffmeisteri* (33.4% to 22.2%), *L. cervix* (25.8% to 8.7%), and *Tubifex tubifex* (4.6% to 0.2%), while the following species indicative of only slight enrichment increased: *Aulodrilus limnobius* (0.0% to 10.3%), and *Aulodrilus pigueti* (1.3% to 12.5%).

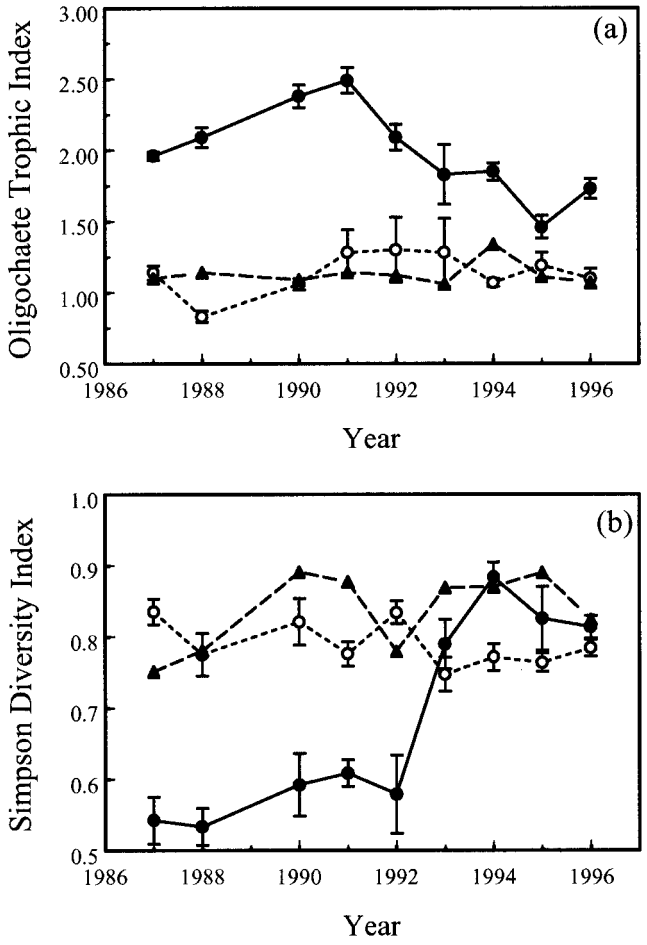


***FIG. 3. Mean (± SE) value of the oligocheate trophic index (a) and Simpson's Diversity Index (b) in silt (•), silty sand (▲), and sand (O) in the inner bay, 1987 to 1996. The indices were calculated from all sampling dates at a particular site, and the mean and standard error were determined for all sites within a particular substrate.***

Densities of chironomids declined in the first few years after the peak in *Dreissena* at sites in the deep water/silt region, but then increased so that the difference in the pre- and post-*Dreissena* periods was not significant (P > 0.05) (Table 5). By 1995 and 1996, chironomid densities were similar to or greater than densities found in the pre-*Dreissena* period. While the total number of species collected in the two periods was similar (16 and 14), there were shifts in proportions of the dominant taxa. The proportion of the following species increased the most: *C. anthracinus* (25.4% to 34.7%), *Chironomus* sp. (2.0% to 17.5%), *Cryptochironomus digitatus* (0.3% to 9.5%), and *Procladius* sp. (3.3% to 7.7%), and the following species declined: *Chironomus semireductus gr*. (52.6% to 25.8%), and *Chironomus plumosus* (12.5% to 0.0%). The latter two species are indicative of highly eutrophic conditions (Saether 1979), and their decline would indicate an improved trophic state, as indicated by the oligochaete trophic index. At these sites, the Simpson Diversity Index increased significantly (P < 0.05) after *Dreissena* colonization, likely as a result of the decline in overall abundance of oligochaetes and the increase in mesotrophic-indicator species (Fig. 3b).

In the outer bay, significant differences in densities between the pre- and post-*Dreissena* periods were not detected for any of the major taxonomic groups at the three sites sampled (P > 0.05). However, after *Dreissena* became established, there was a downward trend in densities of sphaeriids at the 13-m site and *Diporeia* at the 28-m site (Table 5). The downward trend was not apparent until after 1993; if this year was not considered as part of the post-*Dreissena* period, the decline was significant (P < 0.05) for both taxa. Oligotrophic forms dominated the oligochaete community in the outer bay throughout the sampling period. On an annual basis, the oligochaete trophic index at the three sites varied from 0.55 to 1.43, and Simpson's Diversity Index varied from .69 to .90. Differences between the pre- and post-*Dreissena* periods were not significant for either index (P > 0.05).

Minor taxa collected in the bay during the study period included Gastropoda (*Amnicola limosa, Probythinella lacustris, Bythinia tentaculata, Physa* sp., *Pleurocera acuta, Valvata sincera,* and *Valvata tricarinata*), Ephemeroptera (*Caenis* sp., *Hexagenia* sp.), Trichoptera (*Oecetis* sp.), and Isopoda (*Caecidotea racovitzai*). Differences were noted in two of these taxa relative to *Dreissena* colonization. *Oecetis* sp. was more abundant in the post-*Dreissena*

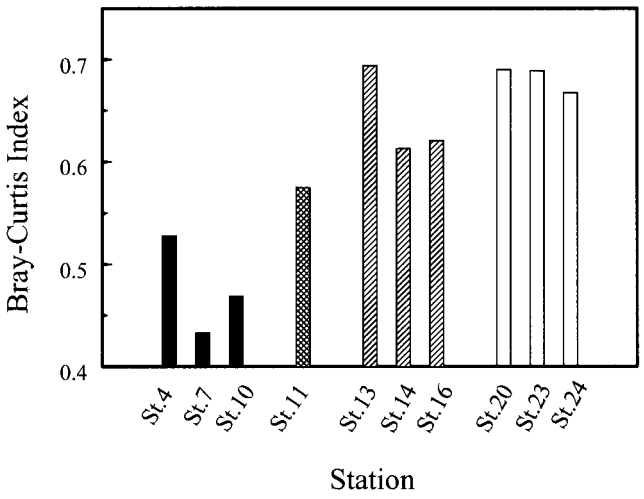


***FIG. 4. Values of the Bray-Curtis Index at the ten sites sampled over the entire 1987 to 1996 period. The index shows the degree of similarity between communities (excluding* Dreissena*) in the pre- and post-*Dreissena *periods (1987 to 1990 vs 1993 to 1996) at each site. solid dark: sites in deep water/silt region in inner bay , cross-hatched: site in mid-depth/silty sand region in inner bay; diagonal: sites in shallow water/sand region in inner bay; solid white: sites in outer bay.***

period at the silty sand site in the inner bay (0/$m^2$ to 10/$m^2$), while *C. racovitzai* was less abundant at the 28-m site in the outer bay (117/$m^2$ to 1/$m^2$).

In comparing communities in the pre- and post-*Dreissena* periods at each of the ten sites, the Bray Curtis Index indicated that communities at sites in the deepwater/silt region changed the most (were least similar), while communities at the outer bay sites changed the least (were most similar) (Fig 4). The index ranged from 0.43 to 0.53 at the former sites and from 0.67 to 0.69 at the latter sites.

### Biomass Trends and Comparisons, Pre- and Post-Dreissena

As found for density, changes in total macroinvertebrate biomass (excluding *Dreissena*) varied by substrate and depth. Biomass at sites with sand substrates in the inner bay was significantly greater (P < 0.05) in the post-*Dreissena* period (1993 to 1996) compared to the pre-*Dreissena* period (1987 to 1990), but differences were not significant at sites with silty sand or silt substrates (P > 0.05). Biomass at sites with sand increased from a mean of 0.10 to 0.43 g/$m^2$ (Fig. 5). This increase was

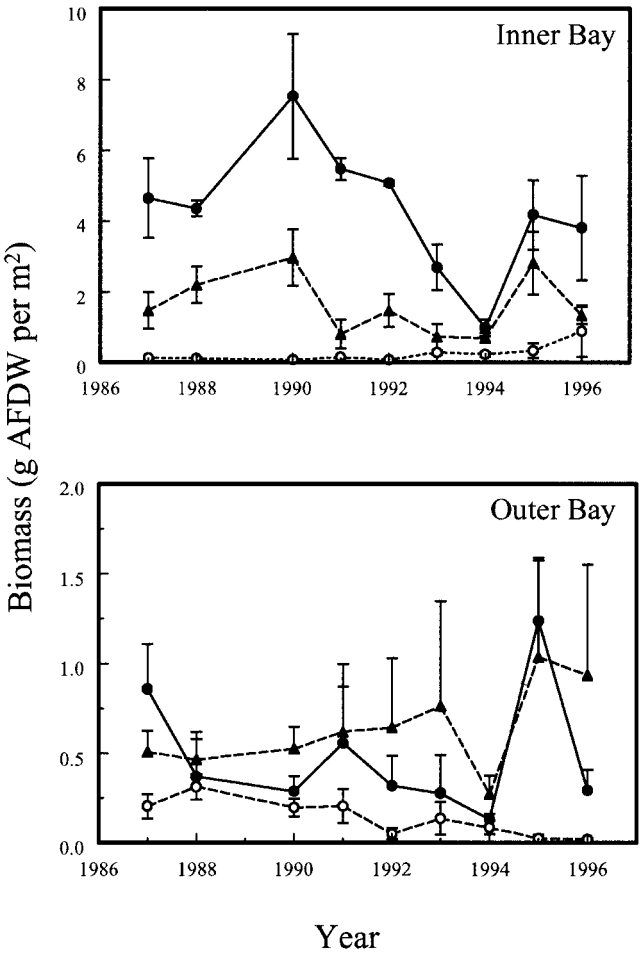


***FIG. 5. Mean biomass (g AFDW/m² ± SE) of benthic macroinvertebrates (excluding* Dreissena*) in the inner bay (upper) and outer bay (lower), 1987-96. inner bay: • = deep water/silt sites, ▲ = silty sand,* O *= sand; outer bay: • = St. 24 (13 m), ▲ = St. 20 (16m ),* O *= St. 23 (28 m ).***

mostly a result of greater numbers of *Gammarus*, although a few large gastropods (*Bythinia tentaculata* and *Pleurocera acuta*) were found in 1996 and not in other years. *Gammarus* accounted for 30% and 56% of total biomass in the pre- and post-periods, respectively. Although not significant, mean biomass at sites in the deep water/silt region decreased from 5.5 to 2.9 g/m², mostly because of lower densities of oligochaetes in the post-*Dreissena* period. Chironomids dominated the biomass at sites in the deepwater/silt region, accounting for 69% of total biomass in the pre-*Dreissena* period and 89% in the post-*Dreissena* period.

In the outer bay, significant differences in total biomass between the pre- and post-*Dreissena* periods were not detected at the two shallow sites (Stations 24 and 20). Large year-to-year variation occurred at both sites during the post-*Dreissena* period (Fig. 5). Biomass at the deeper 28-m site (Station 23) was significantly lower in the post-*Dreissena* period ($P < 0.05$), and this decline can be attributed mainly to decreased numbers of the amphipod *Diporeia* (Table 5).

## DISCUSSION

Trends in densities of the major macroinvertebrate groups from 1987 to 1996 in Saginaw Bay can be put into a historical perspective by examining densities reported in studies over several decades beginning in the mid-1950s (Surber 1954, 1955; Alexander 1963; Shannon *et al.* 1967; Schneider *et al.* 1969; Batchelder 1973; Michigan Department of Natural Resources [MDNR] unpublished data). Densities from previous studies were converted to Ponar equivalents as given in Nalepa *et al.* (2002). An examination of historical trends was limited to the deepwater/silt region since organic materials from both allochthonous and autochthonous sources eventually focus and settle in this region (Robbins 1981), and therefore changes in the macroinvertebrate community most closely reflect shifts in the overall productivity of the system.

In the deepwater/silt region, both oligochaetes and chironomids increased between the 1950s and the 1960s/early 1970s (Fig. 6). These increases were likely a result of increasing nutrient loads and high system productivity (Vollenweider *et al.* 1974). This was also the time period over which the burrowing mayfly *Hexagenia,* a pollution sensitive form, disappeared from the bay (Schneider *et al.* 1969). Phosphorus abatement programs were initiated in the mid-1970s, and total phosphorus loads in the inner bay declined 55% between 1974 and 1980 (Bierman *et al.* 1984). This resulted in a 53 to 61% decline in chlorophyll (20.6 to 12.2 µg/L in spring and 29.1 to 12.2 µg/L in fall) (Bierman *et al.* 1984), a reduction in populations of eutrophic indicator species of phytoplankton (Stoermer and Theriot 1985), and the elimination of nuisance blooms of blue-green algae (Stoermer *et al.* 1983). Further reductions in total phosphorus and chlorophyll were not apparent between 1980 and 1991 (Fahnenstiel *et al.* 1995a).

Despite improvements in water quality, densities of the dominant macroinvertebrate groups, oligochaetes and chironomids, changed little or in-

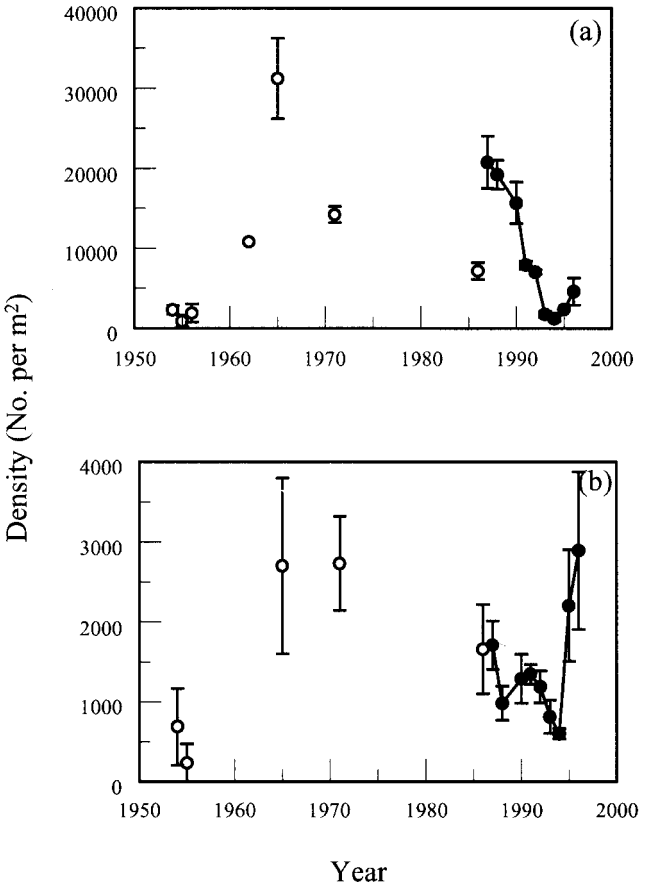


***FIG. 6. Comparison of mean densities (no./m² ± SE) of oligochaetes (a) and chironomids (b) found in this study (•) to densities reported in previous studies (O) at sites in the deepwater/silt region of the inner Saginaw Bay. Densities were taken from the following studies: 1954 (Surber 1954), 1955 (Surber 1955), 1962 (Alexander 1963), 1965 (Shannon* et al. *1967), 1971 (Batchelder 1973), and 1986 (MDNR unpublished data).***

creased between 1971 and 1987 to 1990. This finding is surprising, particularly for oligochaetes, given that other studies in the Great Lakes have found decreases in abundances after abatement programs (Johnson and McNeil 1986, Schloesser *et al.* 1995, Nalepa *et al.* 1998). A close examination of trends suggests that densities of at least oligochaetes were abnormally high in 1987 to 1990 and likely not representative of the post abatement period. For instance, a 1986 survey reported a mean oligochaete density of 7,200/m² in the deepwater/silt region (MDNR unpublished data) (Fig. 6). This value was far less than the mean of 20,800 m² in 1987, just 1 year later. By 1991, densities declined back to 7,900/m². Given the magnitude of this increase and decrease over such a short time period, it is possible that densities were affected by a short-term storm event that occurred in fall 1986. A 100-year flood displaced 8 to 200 cm of surface sediment material from river margins into the bay (Ludwig *et al.* 1993). These organic inputs would have been deposited in the deepwater/silt region and perhaps led to the dramatic increase in oligochaete densities the following year. Densities of tubificid oligochaetes can increase rapidly after periods of high organic sedimentation (nearly a 2-fold increase in just a few months; Lang and Hutter 1981). Consistent with this theory, the highest proportion of immature tubificids over the entire sampling period occurred in 1987 (93%). Subsequent declines, particularly after 1990 but before *Dreissena*, may have been a result of the population returning to levels more at equilibrium with the carrying capacity of the bay prior to this discharge event. Mean annual water temperatures in the inner bay in 1987 and 1988 were higher than in the previous 6 years (McCormick and Fahnenstiel 1999) and this may have also contributed to greater oligochaete recruitment. If densities in 1986 and 1991 are considered to be typical of the post-abatement period, then oligochaete densities declined about 45% from pre-abatement densities found in 1971, and chironomids declined by 40%. However, despite these apparent declines in densities, eutrophic-indicator species of both groups still dominated the community.

Several distinct changes occurred in the macroinvertebrate community just after the peak of *Dreissena* in 1992. At sites in the deepwater/silt region, density and biomass of both oligochaetes and chironomids decreased sharply, even though few mussels were ever found in this region. It is likely that, at least initially, filtering activities of abundant *Dreissena* populations in the sand/shallow water regions of the bay led to diminished organic inputs into the deepwater/silt region, leading to a decline in densities of these two groups. Strayer and Smith (2001) reported a similar pattern in the Hudson River estuary; that is, *Dreissena* populations in shallow-water areas had a negative impact on macroinvertebrate populations in adjacent deepwater areas where no *Dreissena* were present. In inner Saginaw Bay, this response was evident for just a few years after the 1992 peak in *Dreissena*. By 1995 to 1996, oligochaete densities had in-

creased from earlier lows, and chironmid densities were greater than found prior to *Dreissena*. The oligochaete trophic index declined after 1992 and remained lower through 1996, indicating that increased densities in 1995 and 1996 consisted of species reflective of more oligotrophic conditions.

In terms of other taxa, of particular interest was the number of *Hexagenia* spp. collected in the deepwater/silt region of the inner bay. As noted, this pollution-sensitive species was once abundant in this habitat, but disappeared in the 1950s. Over the 9-year study period, five individuals were collected in the inner bay, two in 1990 and three in 1994, and all were found at Station 11 (Nalepa *et al.* 2002). In western Lake Erie, *Hexagenia* returned to former abundances in the early 1990s after a decades-long absence (Edsall *et al.* 1999). *Hexagenia* was not found in Saginaw Bay in the early 1970s (Batchelder 1973; GLRD unpublished), so the finding of a few individuals is noteworthy. Yet a large-scale return to Saginaw Bay, although predicted (Schaeffer *et al*. 2000), had yet to occur through 1996.

There were two clear responses to the establishment of *Dreissena* in the shallow water/sand region: an increase in *Gammarus* and a decrease in Sphaeriidae. Similar to the present study, most other studies have reported a similar response in these two taxa (Howell *et al.* 1996, Haynes *et al.* 1999). *Gammarus* apparently benefits from increased habitat complexity created by *Dreissena* clusters, and from increased food availability generated by mussel biodeposits (Ricciardi *et al.* 1997, Stewart *et al.* 1998). In this study, densities of *Gammarus* in the post-*Dreissena* period (240 to 494/$m^2$) exceeded historical densities (152/$m^2$ in 1956 [J. C. Schneider unpublished data] and 97/$m^2$ in 1971 [Batchelder 1973]). The decline in sphaeriids has been attributed to physical attachment by *Dreissena*, or to competition for food (Lauer and McComish 2001, Strayer and Smith 2001).

In contrast to some studies, we did not observe any changes in densities of oligochaetes or chironomids in response to *Dreissena* in the shallow water/sand region. Relative impacts of *Dreissena* on these two groups are variable and appear to be a function of where samples were collected relative to *Dreissena* clusters. Some studies have shown that densities of these two groups are higher within, or adjacent to, mussel clusters than in surrounding substrates (Karatayev *et al.* 1997, Bially and MacIsaac 2000). Yet other studies have shown that, overall, densities of oligochaetes and chironomids did not change or declined after *Dreissena* introduction (Johannsson *et al.* 2000, Kilgour *et al.* 2000, Strayer and Smith 2001). Mussels do provide more suitable habitat and/or food for these groups but, as argued by Strayer and Smith (2001), local studies within mussel beds neglect changes on a broader spatial scale. The local impact of *Dreissena* on oligochaetes and chironomids is a function of mussel density (Karatayev *et al.* 1997). At sand sites in the inner bay, mussel densities in individual replicates with mussels ranged from 1 to 42,390/$m^2$ (mean = 3,855/$m^2$). Yet even with these densities on a local scale, no relationship between *Dreissena* and densities of oligochaetes and chironomids was observed.

The decline of the amphipod *Diporeia* in the outer bay is consistent with declines in other regions of the Great Lakes after *Dreissena* became established (Dermott and Kerec 1997, Nalepa *et al*. 1998, Lozano *et al.* 2001). A common theory for the decline in *Diporeia* is that mussels are outcompeting *Diporeia* for food resources settling to the bottom, particularly diatoms (Nalepa *et al.* 1998, Dermott 2001). Inconsistent with this theory, at least in the outer bay, is the fact that neither chlorophyll nor diatom biovolumes in the water column declined at Station 23 between 1991 and 1996 (Johengen *et al.* 2000; H. A. Vanderploeg unpublished data). *Diporeia* densities declined at Station 23 just 2 years after *Dreissena* peaked at shallower sites within the outer bay (Stations 19 and 27), yet *Dreissena* was never collected at Station 23 over the entire sampling period. While *Diporeia* has declined in areas where both *Diporeia* and *Dreissena* are found in immediate proximity (Dermott and Kerec 1997), the decline at Station 23 in outer Saginaw Bay provides another example of populations that have declined in areas removed from *Dreissena*, and where food resources are still apparently available to sustain at least some of the population (Dermott 2001).

Based on the relative proportion of the various substrate types within the inner bay (57% sand, 16% silty sand, and 27% silt; Robbins 1981), and mean biomass of benthic communities within each substrate type, system-wide changes in benthic biomass were calculated for each sampling year. The inner bay is a well-mixed, semi-confined system, and thus net gains or losses of benthic biomass may be interpreted relative to overall system productivity. When considered as a whole, biomass of the non-dressenid macroinvertebrate community was affected by *Dreissena* for only a short time period (Table 6). While decreases were apparent immediately after the peak in *Dreissena* in 1992, biomass

increased after *Dreissena* populations apparently stabilized. Mean yearly biomass of 2.30 and 2.72 × $10^9$ g in 1995 and 1996 were not different from values of 2.14 to 3.57 × $10^9$ in 1987 to 1990 prior to *Dreissena*. Thus, the energetic demands of *Dreissena* ultimately did not come at the expense of the non-dreissenid benthic community. The same finding was reported for the western basin of Lake Erie (Johannsson *et al.* 2000), a system similar to inner Saginaw Bay. When *Dreissena* is included, standing stocks of the total benthic community in the inner bay were 2 to 6 times greater in 1993 to 1996 compared to 1987 to 1990 (Table 6). The question remains how the non-dreissenid benthic community can be sustained given the added energetic requirements of the dreissenid population. The system is dominated by detritivores (oligochaetes and chironomids), and conceivably the availability of detrital food did not decline or perhaps even increased. While chlorophyll levels declined 61% in the inner bay after *Dreissena* became established (Fahnenstiel *et al*. 1995a), standing stocks of benthic macroalgae and submersed macrophytes increased because of increased light penetration to the bottom (Skubinna *et al.* 1995, Lowe and Pillsbury 1995). As calculated by Fahnenstiel *et al*. (1995b), a decrease in phytoplankton production was almost compensated for by an increase in benthic algal production, without even considering a potential increase in other benthic producers such as vascular hydrophytes and metaphytonic algae. Moreover, the potential for increased nutrient supply rates resulting from *Dreissena* excretion would enhance growth rates of both benthic and pelagic algae (Heath *et al.* 1995). In addition, large, late summer/fall blooms of the cyanophyte *Microcystis* have been documented in the inner bay beginning in 1994 as a result of selective rejection by *Dreissena* (Vanderploeg *et al.* 2001). When settled to the bottom, this alga may enhance food availability to the benthos, either directly or indirectly through increased bacterial production (Brunberg and Bostrom 1992).

A number of studies have examined macroinvertebrate changes within a specific habitat type, such as within hard-substrate habitats colonized by *Dreissena*, but few have determined changes on a system-wide basis. After *Dreissena* colonized the Hudson River, Strayer and Smith (2001) reported a 10% gain in non-dreissenid biomass at shallow water sites, but a 50% loss at deepwater sites. Based on the proportion that each habitat comprised of the river system, it was estimated that non-dreissenid biomass declined 40% on a riverwide basis. In comparison, a 58% overall decline was found in non-dreissenid biomass in the inner bay within 2 years after the peak in *Dreissena* (1993 and 1994), but then biomass increased such that there was no difference in biomass 3 to 4 years (1995 and 1996) after the *Dreissena* peak when compared to the pre-*Dreissena* period (1987 to 1990). In 1995 and 1996, mean biomass at the shallow-water/sand sites increased by 84% compared to 1987 to 1990, while biomass at the deepwater/silt sites declined by 27%.

***TABLE 6. Biomass (g AFDW × $10^9$) of benthic macroinvertebrates and* Dreissena polymorpha *in inner Saginaw Bay from 1987 to 1996. Values determined by multiplying mean biomass in each substrate type by the proportion each substrate comprised of the inner bay bottom.***

| Year | Benthic Macroinvertebrates | *Dreissena* | Total |
|---|---|---|---|
| 1987 | 2.29 | 0.00 | 2.29 |
| 1988 | 2.14 | 0.00 | 2.14 |
| 1990 | 3.57 | 0.00 | 3.57 |
| 1991 | 2.70 | 9.57 | 12.27 |
| 1992 | 2.43 | 60.44 | 62.87 |
| 1993 | 1.55 | 4.39 | 5.82 |
| 1994 | 0.70 | 3.02 | 3.72 |
| 1995 | 2.30 | 4.01 | 6.31 |
| 1996 | 2.72 | 13.08 | 15.80 |

Even though total non-dreissenid macroinvertebrate biomass did not change as a result of the introduction of *Dreissena* in the inner bay, *Dreissena* likely enhanced the amount of food available to upper trophic levels. When considering macrobenthic forms that are most readily fed upon by many fish such as chironomids, *Gammarus*, and sphaeriids (Wells 1980), the decline in sphaeriids was more than offset by the increase in *Gammarus*, and no long-term changes were observed in biomass of chironomids. For example, yellow perch in the inner bay fed primarily on chironomids in the late 1980s (Schaeffer *et al.* 2000), but also will feed on amphipods when available (Haygood and Margraf 1987). The 5-fold increase in *Gammarus* over most of the inner bay without a corresponding decline in chironomids will likely have a positive effect on this fish species. The assumption, of course, is that *Gammarus* is available to fish and not sheltered from predation within mussel clusters. When con-

sidered as a whole, the fish community in the inner bay shifted to more benthic-feeding forms since *Dreissena* became established (Thomas and Haas 1997). In the outer bay, the introduction of *Dreissena* will probably have a more negative impact on upper trophic levels. Although macroinverteberate biomass at shallower water sites in the outer bay were not affected by *Dreissena*, the decline in biomass at deep-water sites as a result of the loss of *Diporeia* will likely adversely affect some fish species (Pothoven *et al.* 2001).

In summary, it was difficult to determine a clear response of the benthic macroinvertebrate community to phosphorus abatement efforts over the time period of this study. The community in the deepwater/silt region of the inner bay, the best location in the bay to interpret long-term trends, was likely affected by a major storm event that occurred just prior to our initial sampling. This confounded interpretations of abatement efforts. Densities of the two major groups, oligochaetes and chironomids, were likely 45% and 40% lower after abatement and before *Dreissena* colonization, but eutrophic species still dominated each of these groups. After *Dreissena* became established, oligochaete densities initially declined in the deepwater/silt region of the inner bay, but then returned to values near those found in the pre-*Dreissena* period. Also, the oligochaete community shifted to species more indicative of an improved trophic state, and overall species diversity increased. Sphaeriids declined in the shallow/sand and silty sand regions, but *Gammarus* increased. Species diversity in these regions was little changed after *Dreissena* colonization. Despite shifts in community composition, non-dreissenid biomass in the entire inner bay was unchanged relative to biomass found in the pre-*Dreissena* period by the end of the sampling period. In the outer bay, the most significant change was a decrease in biomass at deeper depths as a result of a decline in *Diporeia*. The increase of *Gammarus* in the shallow, nondepositional regions of the inner bay, and the loss of *Diporeia* in the deeper regions of the outer bay have contrasting implications to the food web.

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